

## VOCAL AND TERRITORIAL BEHAVIOR IN THE WHITE-EYED VIREO

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The vocal repertoire and displays of the White-eyed Vireo (*Vireo griseus*) are poorly documented. This paper presents results of a study to elucidate the role of song in the behavior of this species.

Work was done on a population of *V. g. griseus* in Gainesville, Alachua Co., Florida. The White-eyed Vireo in northern Florida is a bird of scrubby second growth, forest edge and early successional marsh-thicket-edge habitats. In the Gainesville area such habitat is plentiful, but it is irregularly distributed in small patches. Much of the suitable habitat lies along the course of Hogtown Creek and cleared right-of-ways under power transmission lines.

The patchy habitat provides a variety of territorial situations. Some males defend lone territories surrounded by unsuitable areas. Others have many neighbors. One such cluster of territories included 11 territorial males in an area of about 14 ha, with a mean territory size of 1.3 ha. In crowded areas agonistic encounters were relatively frequent.

I color-banded a part of the above local population to study the singing behavior of territorial males as well as their offspring. Territoriality and the associated agonistic behavior were studied; little courtship behavior was observed. During the spring and summer of 1977 and 1978 a total of 66 individuals was captured, measured, color-banded and released. These individuals were observed and tape recorded on subsequent visits.

### METHODS

Nylon mist nets were used to capture vireos attracted to tape playback of conspecific song. On occasion a mounted White-eyed Vireo model was placed near the speaker. The taped songs were played back on a Uher CR 134 cassette recorder, using a composite tape of White-eyed Vireo songs recorded from various males in the southeastern U.S. Each study bird was banded with a U.S. Fish and Wildlife Service aluminum band as well as 3 colored plastic bands arranged in a unique combination. The sex of each adult was determined by the presence of an enlarged cloacal protuberance (males) or a functional brood patch (females). Young birds could not be sexed other than by observing their behavior. Birds during their first year of life are referred to as "hatching-year" birds.

Tape recordings of the vocalizations of marked birds were made using a Nagra III open reel recorder and a Sennheiser 805 unidirectional microphone at a tape speed of 19 cm/sec. Audiospectrographic analyses were made using the Kay Elemetrics 7029A Sona-Graph. All of the tapes made during this study have been deposited in the Bioacoustics Archive of the Florida State Museum, Gainesville, Florida. Some motion pictures were taken with a GAF ST602 super 8mm movie camera and analyzed using a Bell and Howell 1623Z stop-action projector.

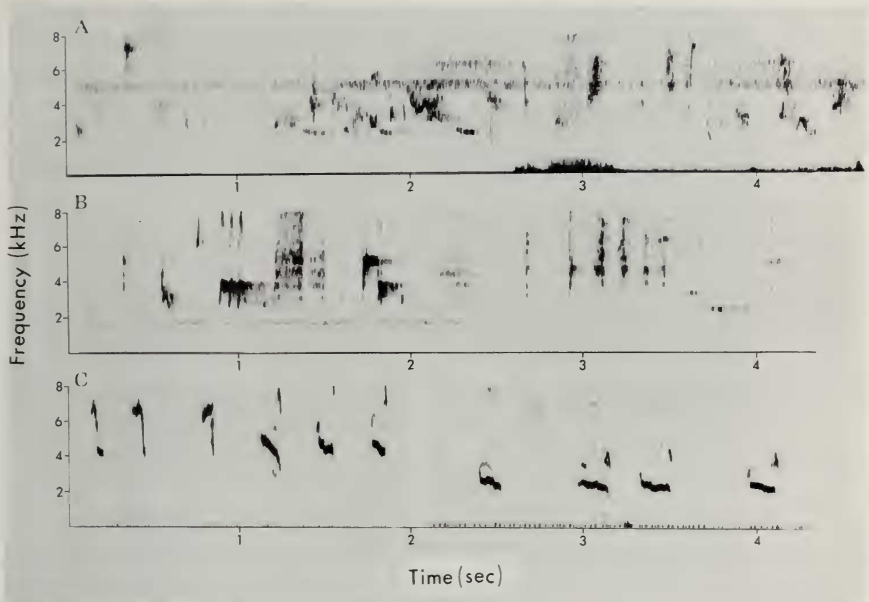


FIG. 1. Wide-band audiospectrograms of White-eyed Vireo vocalizations: A. the subsong of a hatching-year male; B. rambling song of an adult male in the presence of an adult female; C. distress squeals of an adult male vireo in the hand.

## RESULTS

*Subsong and rehearsed song.*—Subsong in this species is characterized by soft warbling and poorly defined notes. The song is more loosely organized than adult song and is more or less continuous (Fig. 1A). Some of the notes have a harsh chatter-like quality typical of the other adult vocalizations (“chatter” vocalization, “rambling song”).

Within 2 weeks subsong is replaced by rehearsed song. This is an intermediate stage between the unorganized warbling subsong and typical discrete adult song (*sensu* Lanyon 1960). Males sing rehearsed song for a period of several weeks during which this song gradually evolves into discrete song.

Male White-eyed Vireos begin to sing at an early age. The earliest date that I observed subsong was 1 June. The singing male was positively identified as a hatching-year bird (dark iris and juvenal plumage). The earliest egg date I have for this region is 10 April ( $N = 6$  clutches). With an incubation period of 15 days (Bent 1950) and a nestling period of 11 days (estimate) this bird probably fledged no earlier than 6 May. Many

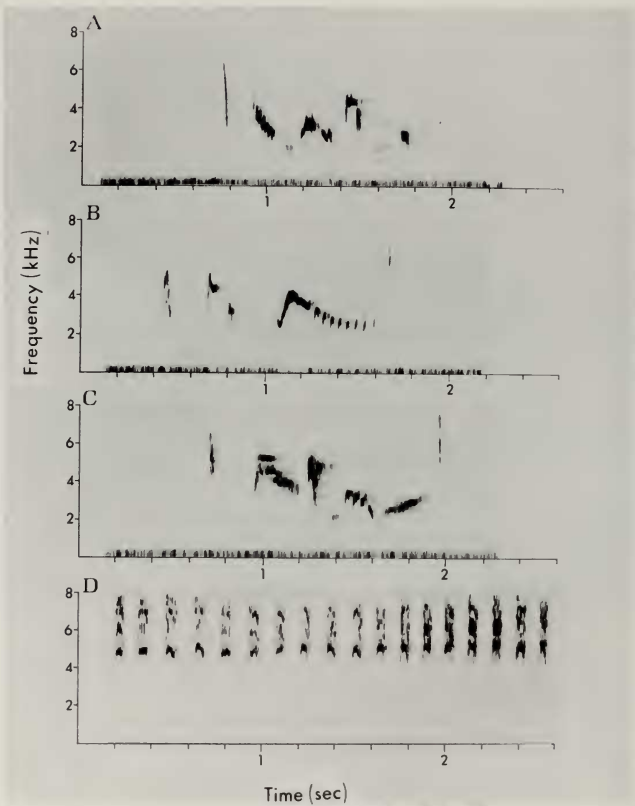


FIG. 2. Wide-band audiospectrograms of White-eyed Vireo vocalizations: A, B, and C. 3 examples of adult male discrete song recorded from 1 individual's repertoire; D, agonistic chatter vocalization.

birds fledged by early May. I thus estimate that some young males begin subsong within 2 weeks of fledging.

Hatching-year White-eyed Vireos often follow their fathers around the home territory. These birds are occasionally fed by the adult male. Sometimes the hatching-year birds cooperate in the defense of the home territory. For example, playback experiments elicit the same agonistic behavior from young birds as they do from adults. Some young birds (presumably males) sing rehearsed song simultaneously with their fathers' discrete song. Others use only the chatter vocalization and are assumed to be hatching-year females. Young birds may also display using head-forward postures, displacement preening and supplanting attacks (described later in text).

Late in the summer young males sang more or less typical "discrete song" with shorter than normal inter-song intervals. These first-year birds also sing the rambling song. In fact, they seem to use it more frequently than adults males. Birds of the year continue to sing after dispersal from the home territory and may establish and defend a vacant or abandoned territory. By the end of August the song of young males is typical of discrete song. Few, if any, adult males are still singing at this time.

*Discrete song.*—The discrete song is given only by males. It is composed of several loud whistled notes combined with sharp tick notes and short buzzes. The song often begins with a high pitched or strongly inflected note, includes a series of rapidly uttered complex notes and concludes with another sharp or inflected note. The song is short ( $\bar{x}$  = 1.02 sec, N = 213 song patterns) and relatively loud. It has often been described as having an explosive character (Fig. 2A–C).

Discrete song is delivered at a rate of 10–20 times per min depending upon the activity state of the singing male. Song can be heard throughout the day, but I observed a decided peak in the 2 h following sunrise. During the 1977 season, I first heard song in late February. Song persisted well past the nesting period, with sporadic adult song until at least 3 July.

The repertoire of each male contains a number of different song patterns or motifs. Each of these is a reproducible song of fixed structure (Fig. 2). The mean repertoire size recorded from 41 color-banded males was 5.2 patterns. Two males had repertoires of 13 motifs. I believe that most males sing at least 10 patterns and the low average reflects insufficient sampling. Different motifs used by 1 male are rarely very similar. Individual song figures or notes, however, occur repeatedly in a particular male's repertoire. A male usually sings only 1 or 2 motifs during a particular song bout. A song bout is 1 continuous series of song motifs uttered at a regular rate, usually for 5–10 min. Song bouts are separated by longer pauses from 5 min to several hours. One male sang 99 repetitions of 1 motif before pausing. Less than 5 min later the same male sang 41 renditions of this motif before changing patterns. Males increase the variety in their song performance when responding to an intruding male or playback of a conspecific's song. Recordings from 8 color-banded males were analyzed before and after playback. These males averaged 1.8 motifs in 5-min song bouts recorded before playback and 5.5 motifs in 5-min bouts immediately following playback.

Discrete song is used primarily in territorial defense. Adult territorial males spend much of each day during the breeding season patrolling the territory while singing. An intruding male is often located by song, and song itself plays an important role in the agonistic sequence. During counter-singing bouts, territorial males do not attempt to "match" motifs, as

sometimes happens in other species that sing complex repertoires (Hinde 1958, pers. obs.).

*Rambling song.*—This song is longer than typical song and may last 5–10 sec or more. The structural character of rambling song is also distinctive. Rambling songs are composed of some typical song notes, some notes suggestive of the aggressive chatter as well as other harsh staccato notes (Fig. 1B). The rambling song is usually delivered at a lower amplitude than discrete song. It is interesting to note that hatching-year males utter this song as often, or more often, than discrete song during their transition from rehearsed to discrete song. Rambling song is used in an epigamic context. When this song was heard from a male not engaged in territorial defense, it was frequently followed by approach of the female and copulation. After copulation the male ceases rambling song. After a pause of 1–5 min the male begins to sing discrete song and patrol his territory.

An analogous song type has been described for the Red-eyed Vireo (*V. olivaceous*). In this species the male makes a fanned-tail display while singing a warbling, continuous version of the song (Lawrence 1953). This Red-eyed Vireo display was observed during courtship and preceded copulation. The Bell's Vireo (*V. bellii*) also sings a run-on song during courtship (Nolan 1960, Barlow 1962). Nolan (1962) describes a continuous "faint squeaky song" in the courtship of Red-eyed and Yellow-green (*V. o. flavoviridis*) vireos.

*Chatter vocalization.*—The chatter vocalization is a rapid series of harsh noisy rasp sounds composed of wide frequency band pulses in an irregular rhythmic pattern (Fig. 2D). The call may be more or less continuous, but is often given in short intense bursts, lasting 3–5 sec. Similar notes are incorporated into subsong of juveniles and rambling song of adult males.

This vocalization is uttered in agonistic contexts, especially in territorial encounters between males. The most frequent response to taped playback of discrete song with simultaneous presentation of a model includes this call. The male ceases singing, assumes an alert sleeked posture, then utters the scolding chatter. The male stands horizontally, erects the crest feathers slightly and chatters. During the utterance the feathers of the throat bulge out (Fig. 3E). This chatter display may be analogous to the head-forward display that is accompanied by the *myaah* call in Red-eyed Vireos (Barlow and Rice 1977).

The chatter is also given in response to "pishing" sounds made by a person or when mobbing a potential predator, and by the female in response to a distress squeal of her mate. The chatter is the most common call of adult female White-eyed Vireos. Females often given this call while the male is engaged in a counter-singing bout with a neighbor, and occasionally in response to taped playback of the discrete song.



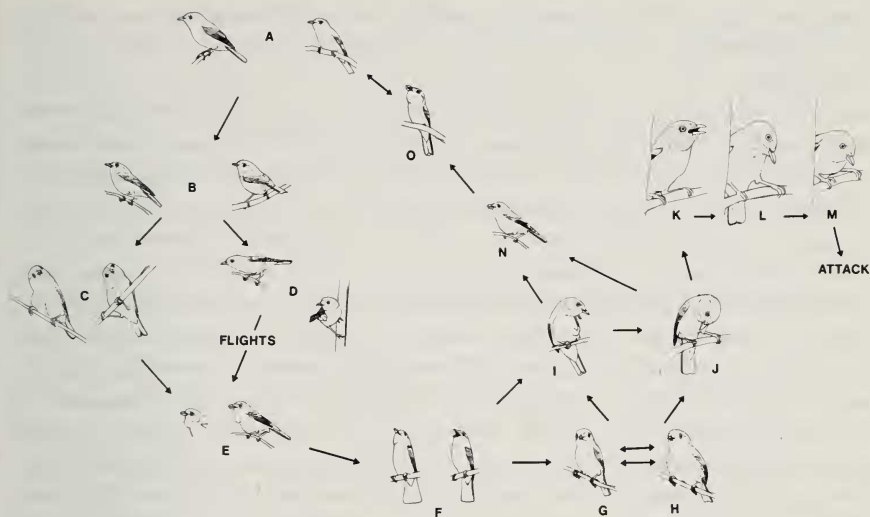


FIG. 3. An ethogram of the territorial response of a male White-eyed Vireo drawn from stop-frame motion picture analysis: A. relaxed posture; B. alert posture; C. sidelooking; D. flight intention movements; E. chatter vocalization; F. high-intensity song; G, H. the sleek-fluff display; I. displacement preening; J. redirected attack; K, L and M. a sequence from nervous song through attack; N. chatter vocalization; O. discrete song.

*Distress squeal.*—Captured White-eyed Vireos occasionally utter a sharp dissonant and repetitive squeal (Fig. 1C). This call is surprisingly loud and has a penetrating quality. It may serve to startle a would-be predator, or summon the assistance of a mate.

*Alert posture.*—When a territorial male hears the song of a conspecific within his territory he assumes an alert posture. This behavior also appears in response to the aggressive chatter call or the distress squeal. In the alert posture the body feathers are addressed to the body (Fig. 3B,D).

*Flight intention and supplanting attack.*—I have given the name flight intention movements to various postures associated with high anxiety (Fig. 3D). These postures resemble the alert pose, but include exaggerated neck movements in the intended direction of flight and are often accompanied by wing flicks. Flight intention may act as a threat behavior. Flight intention movements, including wing and tail flicking, have also been observed in Bell's Vireo (Barlow 1962). Barlow states that flight intention indicates an internal conflict between the tendencies to flee, attack or court another vireo. Short flights over the head of the intruder often follow the flight intention pose. The bouts of flight are sometimes accompanied by the chatter call. If these flight threats and chatter fail to dislodge an intruder

a supplanting attack will occur. As with Red-eyed Vireos (Barlow and Rice 1977) supplanting attacks occur between males at poorly defined territorial boundaries.

*Sidelooking.*—One behavior that has not been mentioned by other authors is sidelooking. This involves a tilting of the head towards the intruder-stimulus (Fig. 3C). It may represent actual monofocal staring or perhaps listening. The behavior is exaggerated and is not always directed at the stimulus. It is possible that this is merely intense search behavior.

*Sleek-fluff display.*—When a male White-eyed Vireo is confronted with a persistent intruder or model he will frequently present a sleek-fluff display. I have given this name to alternate sleeking then fluffing of the body feathers in a deliberate manner at intervals of about 1 sec (Fig. 3G–H). This action is effective in producing a flash of pale plumage which can be seen even through fairly dense vegetation. The sleek-fluff display does not appear similar to the ruffled-spread body feather action exhibited by other vireo species during the “swaying display” described by Nolan (1962) and others. It may, however, be related to the ruffled feather tail-fanning of agonistic encounters of Bell’s Vireo (Barlow 1962).

*Displacement preening.*—When an intruder does not leave in response to the chatter calls or overhead flights, displacement preening activities may occur. This behavior resembles typical preening but includes vigorous pecking at the feet or perch. Displacement preening is often accompanied by nervous sidelooking. The pecking redirected attack behavior probably results from a conflict of motivation.

*Grappling.*—When supplanting attacks fail to chase an intruding vireo from the territory an actual contact fight may occur. The birds fly toward each other, interlock feet and beat each other with their wings. They also peck at their opponent as they tumble to the ground. The term “grappling” was applied by Barlow and Rice (1977) to this attack behavior.

*Integrated territorial response.*—The response of a resident White-eyed Vireo to an intruder is predictable. There is a sequence of different actions dependent upon the nature of the intruder-stimulus. The responses range in intensity from initial interest to final attack (Fig. 3).

Initial interest response is given by a male that hears the song of the species in his territory. The male will assume the alert posture and cease song. He then flies to the general area of the intruder, remaining fairly high in the canopy. If the intruder remains in the area the male will exhibit signs of increased excitement and utter the chatter vocalization (Fig. 3E).

In the second phase of response, the male may resume singing or continue chattering while searching actively. The song is a high-intensity song, uttered from a stiff erect posture (Fig. 3F). The search activity includes exaggerated sidelooking (Fig. 3C), flight intention (Fig. 3D), short

flights over the intruder, or a supplanting attack. The intruder usually departs, but if it remains the resident male may display exaggerated preening activity (Fig. 3I) and pecking at his own feet or a nearby twig (Fig. 3J). The sleek-fluff action may also occur (Fig. 3G-H). Barlow (1962) describes an incident in which a White-eyed Vireo used "maximal tail-fanning" prior to attack. Although I have noticed that the tail is partly spread, then closed, in rapid succession during high-intensity song (Fig. 3F) I have not witnessed other tail-fanning.

If none of the above actions succeed in displacing the intruder the male may fly at his opponent and attack, with bill and feet. Grappling lasts only seconds and is accompanied by vigorous agonistic chatter from both individuals. The defeated bird then flies off silently, and the victor will preen or commence discrete song at a moderate intensity (rate about 1 song/5 sec).

The response of a resident female is not nearly so intense as that of her mate. She may approach and search actively, often uttering the agonistic chatter. I have not observed displacement preening, pecking, sleek-fluff, discrete song or rambling song from a female.

When a tape recorder is the intruder-stimulus the male vireo will respond in the typical manner. The search activity is very intense but no attack occurs. Even the presence of a mounted vireo fails to elicit an attack, although close approach does occur.

#### DISCUSSION

It is instructive to compare the behavioral repertoire of the White-eyed Vireo observed in this study to that described for other species of the genus. The chatter vocalization serves as the principal agonistic and localization call in this species and is analogous to the *myaah* call of the Red-eyed Vireo, the *ehhh* call of the Philadelphia Vireo (*V. philadelphicus*) (Barlow and Rice 1977) and the *chee* call in Bell's Vireo (Barlow 1962). The rambling song probably serves primarily in courtship of White-eyed Vireos and is similar to the run-on warbling song of Red-eyed and Yellow-green vireos (Nolan 1962) and the congested song of Bell's Vireo (Barlow 1962). Behaviors, including an alert posture, head forward threat, displacement preening, supplanting attack and grappling are shared with other vireos. Barlow (1962) describes tail-fanning for the White-eyed Vireo. I have not observed it during this study. Barlow and Rice (1977) describe an agonistic "bubble" song in Philadelphia Vireos not observed in Red-eyed or Bell's vireos. I did not hear any "bubble" song during the current study.

I have described 2 displays that have not been mentioned by other authors. The first is an exaggerated sidelooking which appears during



intense search behavior. The second I named the sleek-fluff display. The sleek-fluff display may be analogous to the ruffled tail-fanned posture of other species (Barlow 1962). Both of these displays are associated with agonistic encounters between males; they share spread body plumage, presumably to make the displaying individual appear larger or more formidable. In the sleek-fluff display the tail is often partly spread, though not as widely as in the Red-eyed Vireo's tail-fanned posture.

The development of song behavior has not been described for any species of vireonid. I have presented some evidence that song learning occurs relatively early in the White-eyed Vireo. Preliminary analysis of the songs of 3 hatching-year White-eyed Vireos indicates that most of the motifs in their repertoires are identical copies of their fathers' motifs (9 of 12 motifs). The other motifs are shared with immediate territorial neighbors. Adkisson and Conner (1978) describe the incorporation of calls from a variety of other species into the songs of White-eyed Vireos.

#### SUMMARY

This paper presents initial results of work on a population of White-eyed Vireos in Gainesville, Florida. The study involved color-banding a large part of the local population to study song in territorial males and their offspring. During the spring and summer of 1977 and 1978 over 60 territorial males were captured, measured, color-banded and released. These individuals were observed and tape recorded on subsequent visits.

Discrete song is the typical species-specific song. Each male sings 5-15 different song types with a mean length of 1.02 sec. Rambling song is a long, loosely structured song that includes many harsh notes. Rambling song was observed in epigamic contexts and has related counterparts in repertoires of other *Vireo* species. The chatter vocalization is a series of short harsh sound bursts uttered during agonistic encounters between males, or by a female in response to an intruding male's song.

I have described 2 displays that have not been mentioned by other authors, sidelooping and sleek-fluff. Exaggerated sidelooping appears during intense search behavior. The sleek-fluff display may be analogous to the ruffled tail-fanned posture of other species.

Several displays common to other vireos were observed including, alert posture, head-forward threat, displacement preening, supplanting attacks and grappling. Song learning is apparently very rapid. Young birds sing fully developed songs by the end of their first summer.

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## COLOR PLATE

The color plate Frontispiece of Goldie's Bird of Paradise (*Paradisaea decora*) has been made possible by an endowment established by Dr. George M. Sutton.